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NOTES ON PSITHYRUS, WITH RECORDS OF TWO NEW AMERICAN HOSTS.¹

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In Franklin's monumental work, "The Bombidæ of the New World," we have a taxonomic outline of the American bumblebees, equal, if not superior, to similar works on the European species. One is rather disappointed, however, on comparing our knowledge, or rather lack of knowledge, concerning the habits of the American species with the interesting accounts of the habits of the European species given by men like Hoffer and Sladen. What we do know about the habits of our North American species we owe chiefly to the efforts of Putnam, Franklin, and Frison, but the field is so large that the surface has hardly been scratched. This is especially true of one of the subdivisions of our *Bremidæ*,² the genus *Psithyrus*. Of the 13 or 14 species of *Psithyrus* described from the New World, the hosts of only two have thus far been recorded. On July 7, 1914, Sladen ('15), at Agassiz, British Columbia, dug up a nest of *Bremus flavifrons* Cresson, victimized by *Psithyrus insularis* Smith, and two years later Frison ('16) recorded that, during the summers of 1910 and 1915, he had repeatedly found the nests of *Bremus pennsylvanicus* De Geer infested by *Psithyrus variabilis* Cresson. To these two records the writer wishes to add two others, those for *Psithyrus laboriosus* Fabricius and *Psithyrus ashtoni* Cresson.

Before going into detail, however, it seems desirable to give a brief résumé of the structure, life history, and habits of these social parasites, as we know them chiefly from the work of Kirby (1802),

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 201.

² In using *Bremus* and *Bremidæ* instead of the familiar *Bombus* and *Bombidæ*, the writer follows Frison ('19) who in a recent paper pointed out the reasons for making this change (cf. also the extensive paper by Morice and Durrant ('14) on this subject).

Smith ('55), Hoffer ('81, '88), Sladen ('99, '12, '15), and Frison ('16, '21).

STRUCTURE.

Both sexes of the genus *Psithyrus* so closely resemble those of the genus *Bremus* that anyone, other than a specialist, would see no difference between them; and even the specialist sometimes has difficulty in determining whether a certain male is a *Bremus* or a *Psithyrus*, so that it has occasionally happened that *Bremus* males have been described as *Psithyri*, and *vice versa*. It is quite easy, however, to tell a *Bremus* female from a *Psithyrus*, because the latter lacks *corbiculae*, or pollen baskets, a fact which was first noticed by Kirby (1802, I., pp. 209, 210). Illiger (1806, p. 173), suspecting a corresponding difference in habits, separated them from the true bumble-bees, and Newman ('34, p. 404) later gave the group the generic name of *Apathus*. This term held sway for over 40 years, when it was discovered that the name *Psithyrus* had been given to the group by Lepeletier in 1832 (p. 273).

LIFE HISTORY AND HABITS.

According to Hoffer ('88) and Sladen ('12), the young *Psithyrus* queen, like the young *Bremus* queen, hibernates in the ground, but reappears somewhat later in spring than does the latter. Having no apparatus for collecting pollen, she is unable to found a colony of her own, as does the *Bremus* queen, but, like the European cuckoo and some of our American cowbirds, perpetuates her kind by entering, and laying her eggs in, the nests of her more industrious cousins of the genus *Bremus*. The latter, like the dupes of the European cuckoo, rear the larvæ of these lazy guests instead of their own. As will be seen later, these latter, at least those in the earlier stages of development, are probably systematically destroyed by the *Psithyrus*.

That the *Psithyrus* queen does not always gain admittance to a *Bremus* colony without a struggle is indicated by the frequent discovery in bumble-bee nests of dead or disabled *Psithyri* or *Bremi*, or both, and is confirmed by direct observation when a *Psithyrus* first enters, or is placed in, a *Bremus* nest. In these encounters the *Psithyrus* has a great advantage over the individual members

of the *Bremus* colony. She has a powerful sting, and her integument is so thick that her opponents are unable to penetrate it with their stings. But, like Siegfried and Achilles, the *Psithyrus* is vulnerable in certain places—*e.g.*, the neck—and it is chiefly for this reason that she is not always successful.

However, as already indicated, a *Psithyrus* queen sometimes does gain admittance to a *Bremus* colony without losing her life and may remain with the colony until she dies. Here the question arises: What is the attitude of such a *Psithyrus* queen and the rightful owners of the nest to each other? The two foremost European authorities on the subject do not agree on this point. Hoffer ('81, '88), who studied the habits of the European *Psithyri* more extensively than any other investigator, repeatedly found the *Psithyrus* queen living peacefully with the members of the *Bremus* colony, including the host queen. Sladen ('99, '12, '15), on the other hand, claims that the *Psithyrus* queen, at least those of *Psithyrus rupestris* Fabricius and *Psithyrus vestalis* Foucrier, always kills the *Bremus* queen,¹ either at the time the *Psithyrus* queen enters the nest or a few days later, when the *Psithyrus* is about to begin egg-laying. After the *Psithyrus* has committed this murder, the *Bremus* workers, according to Sladen ('12), constantly watch for an opportunity to avenge their mother by killing the usurper. He (p. 60 ff.) very vividly describes this phase in the life history of the *Psithyrus* queen and the afflicted bumble-bee colony as follows: "It is the practice of the *Psithyrus* female to enter the nest of the *Bombus*, to sting the queen to death, and then to get the poor workers to rear her young instead of their own brothers and sisters.

"The way in which the *Psithyrus* queen proceeds in order to ensure the success of her atrocious work has all the appearance of a cunning plan, cleverly conceived and carried out by one who not only is a mistress of the crime of murder, but also knows how to commit it at the most advantageous time for herself and her future children, compelling the poor orphans she creates to become her

¹ On July 14, 1911, Sladen ('12, p. 70) took a nest of *Bremus hortorum* Linnæus, containing 49 workers of *B. hortorum*, and 16 young queens and 2 males of *Psithyrus barbutellus* Kirby. From this rather meager evidence he concludes that *Ps. barbutellus* is probably "parasitic in the same deadly way as *Ps. rupestris* and *vestalis*."

willing slaves. . . . Her first care is to ingratiate herself with the inhabitants, and in this she succeeds so well that the workers soon cease to show any hostility towards her. Even the queen grows accustomed to the presence of the stranger, and her alarm disappears, but it is succeeded by a kind of despondency. Her interest and pleasure in the brood seem less, and so depressed is she that one can fancy she has a presentiment of the fate that awaits her. It is by no means a cheerful family, and the gloom of impending disaster seems to hang over it."

The hostile attitude of the *Bremus* workers toward the *Psithyrus* which has killed their mother (in one case weeks before) is described by Sladen ('12, pp. 256, 277) as follows: "It was clear that the workers deposed the *Psithyrus* queen, and I think that this was the culminating act in a revolt that the queen had all along found it difficult to repress. . . . It appears that when the [*Bremus*] colony is populous the [*Psithyrus*] *rupestris* [queen] will lose her life unless she maintains constantly her rule of repression."

Though interesting, this account of the behavior of the *Psithyrus* queen and the victimized *Bremus* colony toward each other is not only opposed by the earlier work of Smith ('55, p. 210) and Hoffer ('81, '88), but also by recent observations on the habits of some of our American *Psithyri*.

During the summer (June 24 to August 12) of 1921 the writer located 14 *Bremus* colonies, 13 of which were placed in observation boxes a day or two after they were discovered. They were then transferred to the Bussey Institution, where they were kept under observation for periods varying from one to four months. Each box was provided with a glass cover and an opening which communicated with the outside world through holes in boards placed below the screens of three of the windows (one on the second and two on the third floor) of one of the Bussey buildings. Nearly all of the colonies flourished, some producing hundreds of young queens and males. On August 9, colony No. 13 (*B. affinis*) was dug up after much effort, the tunnel being over seven feet in length. The nest was about three feet below the surface and contained the old queen and about 100 workers of *Bremus affinis* Cresson, and the old queen, 3 young queens, and 6 males of

Psithyrus ashtoni. The comb consisted of numerous empty *Bremus* and *Psithyrus* cocoons and a large quantity of *Psithyrus* brood in various stages of development. This colony was kept under observation until September 26. From August 9 until September 14 the nest was examined at least twice a day. Once a week every worker was caught, so that the young *Psithyri*, which had hatched during the preceding week, could be collected without incurring the wrath of the colony. Thereupon the young *Psithyri* were placed in a box and fed with honey and pollen until their pile attained its full color. In this way 29 males and 61 females of *Ps. ashtoni* were collected from this *Bremus*-*Psithyrus* colony, but a considerable number of males, and perhaps a few females, probably made their escape during the last few days preceding the weekly collections.

Despite the fact that the abdomen of the *Bremus* queen was much distended, and that she was seen to lay eggs on August 10 and on subsequent days, not a single *Bremus* queen, male, or worker hatched. As the nights became colder during the early part of September, the *affinis-ashtoni* colony, which by this time had dwindled down to about a dozen individuals, gradually died off. On September 12 the old *Psithyrus* queen was found dead in the nest, two days later the *Bremus* queen was missing, and the last worker died on September 26.

In this case the *Psithyrus* queen must have gained admittance to the *affinis* nest during or before the first few days of July. The *Psithyrus* and the *Bremus* queen, therefore, lived together for at least two months. During the time they were under observation (August 9 to September 12) the two queens did not show the least antagonism, nor did any of the other members of this *Bremus*-*Psithyrus* colony exhibit the slightest sign of hostility toward each other.

The fact that no young bees developed from the eggs laid by the *Bremus* queen corroborates similar observations by Hoffer ('88)¹

¹ This author ('88, p. 101) reports two exceptions to this rule. On September 1, 1880, he took home a nest of *Bremus variabilis* Schmiedeknecht containing the old queen and 15 workers of *B. variabilis*, and 8 females and 10 males of *Psithyrus campestris* Panzer. During the next few days, 4 more males and 9 females of *Ps. campestris*, and 2 males and 3 females of *B.*

and Sladen ('12). Here the question arises: What becomes of the eggs laid by the *Bremus* queen, or workers, of a *Psithyrus*-ridden nest? Hoffer ('88) considers it probable that the young larvæ which hatch from them are eaten by the young *Psithyrus* larvæ. However, Sladen ('12) actually saw a *Psithyrus* queen devour the eggs of *Bremus* workers, and believes that she always disposes of them in this way. He (p. 257) also thinks it is probable that the race-suicidal habit of the workers of *Bremus lapidarius* Linnæus, which sometimes eat the newly laid eggs of their mother, is associated with the parasitism of *Psithyrus*. He believes that the workers which devour the eggs of their stepmother perpetuate this instinct through their sons. In support of this theory, he states that he has never seen the workers of *Bremus latreillellus* Kirby, "a species that is not preyed upon by any species of *Psithyrus*," molest their mother's eggs. This explanation does not seem plausible. It is a well-known fact (cf. Wheeler, '10) that both queen and worker ants, even of those species which are not molested by parasitic ants, sometimes eat their own eggs. Moreover, the writer has frequently seen the workers of *Bremus fervidus* Fabricius eat their mother's eggs, and this species, as will be shown in another paper, probably does not suffer any species of *Psithyrus* to breed in its nests, a view which is supported by more than twenty records (10 by Putnam, "a large number" by Franklin, and 7 by the writer) of *fervidus* nests, none of which were victimized by a *Psithyrus*.

The question has sometimes been raised as to whether or not the members of the genus *Psithyrus* have any workers. Hoffer ('88, p. 114) answers this question negatively. Among the 61 *ashtoni* females reared by the writer there is a great variation in size (cf. Plate I.), some specimens not exceeding that of medium-sized *affinis* workers. It will also be noticed (cf. Plate I.) that the *Psithyrus* males vary greatly in size. If it is true that the difference between queen and worker of the social *Hymenoptera* is due to a quantitative or qualitative difference in feeding during the *variabilis* hatched from this colony. Four years later (June 24, 1884), one of his sons discovered a nest of *Bremus pratorum* Linnæus, containing the old queen, 2 young queens, 5 males, and 26 workers of *B. pratorum*, and the old queen, 9 young queens, and 4 males of *Psithyrus quadricolor* Lepeletier.

larval stage, then these small *Psithyrus* females are comparable to *Bremus* workers. Whether or not they are more inclined to work than the full-sized *Psithyrus* females remains to be determined.

Sladen ('12, pp. 62, 63) believes that the *Psithyrus* queen, like a dog, is largely guided by scent in locating the nests of her victims, and is much more likely to find them when they have a short tunnel. In support of this view, he points out that most of the nests containing *Psithyri* which he dug up had tunnels not exceeding fifteen inches in length, and that in no case were they more than two feet long, and he thinks it is probable that species like *Bremus terrestris* Linnæus and *Bremus lapidarius* often have longer tunnels than other species in order to escape the *Psithyrus*. That this precaution is no absolute insurance against the invasion of *Psithyrus ashtoni* is indicated by the *affinis-ashtoni* nest with a tunnel of more than seven feet.

In a recent paper Frison ('19), on the basis of geographical distribution, expressed the belief that *Ps. laboriosus* "is an inquiline in the nests of *B. fervidus* or *B. vagans*." The writer is pleased to be able to confirm the last part of this prediction. On August 2, colony No. 11 (*B. vagans*) was dug up and transferred to a third-story window in one of the Bussey buildings. Eight days later (August 10) the writer found that a *Ps. laboriosus* queen had gained admittance to the nest. At this time the *vagans* colony consisted of the old queen, about 50 workers, and several males. In the afternoon of the same day the *Psithyrus* queen was observed in the act of tearing open a mass of wax containing small *Bremus* larvæ, so that three of the latter rolled to the bottom of the nest box, leaving the remaining four widely exposed. As usual, these larvæ were thrown out of the nest a few minutes later by the *Bremus* workers. About 5 P.M. the *Psithyrus* queen began to gather wax from the cocoons and built a small cell in which, about 7 P.M., she laid several eggs. As each egg was deposited the sting of the *Psithyrus* penetrated the wall of the cell.

Hoffer ('88), who, despite his extensive observations, never saw a *Psithyrus* oviposit, states (p. 100) that the *Psithyrus* queen lays her eggs in pollen masses in which *Bremus* eggs, or larvæ, are already present. This, as is shown by the observations of Sladen ('12) and of the writer, is not true of *Ps. rupestris* and *Ps. labori-*

osus, and, judging from the oviposition of the members of the genus *Bremus*, is rather improbable of any of the *Psithyri*. The observations of Sladen ('12) and of the writer also indicate that Hoffer's ('88) surmise that the *Psithyrus* larvæ, at least those recently hatched, devour the larvæ of their host,¹ is not true of all, if of any, members of the genus *Psithyrus*.

Six of the eggs laid by the *Ps. laboriosus* queen developed into queen larvæ which spun their cocoons about August 25. On September 7, a *Ps. laboriosus* queen emerged from one of these. The queens in the other five cocoons were heavily parasitized by *Melittobia* sp. and did not hatch. Nor did any of the *Bremus* eggs and larvæ develop which were present in the nest when the *Psithyrus* queen gained admittance to this colony. Whether or not, in this case, the *Bremus* queen laid any eggs² after the appearance of the *Psithyrus*, could not be determined.

Hoffer ('88, pp. 104, 105) states that whenever the old *Psithyrus* queen dies, while her larvæ are still very young, the latter, as a rule, likewise perish, and he considers it probable that the *Psithyrus* queen forages and contributes something to the support of her offspring, at least during their early larval stages. The latter is not true of *Psithyrus ashtoni*, and, as the observations of Sladen ('12, p. 65) and of the writer indicate, is also improbable of other species. Both the *Ps. laboriosus* and the *Ps. ashtoni* queen were always at home, and, as regards the latter, foraging was out of the question. She was able to fly but a few feet at the time the *affinis-ashtoni* colony was taken, and still her brood, including some newly hatched larvæ, was in a flourishing condition. It is probable, therefore, that the *Psithyrus* larvæ which Hoffer ('88) had under observation died from other causes.

The behavior of the *Psithyrus laboriosus* queen and the *vagans* colony to each other was the same as that of the members of the *affinis-ashtoni* colony, except during the first three or four days.

¹ This is true of the larvæ of certain solitary parasitic bees, as Verhoeff ('92), Höppner ('04), and Graenicher ('05) have shown.

² Sladen ('12, p. 69) claims that a large number of workers in a *Psithyrus*-ridden colony become fertile. This was true of my queenless *B. impatiens* colonies, but none of these would accept a *Psithyrus* queen. However, in my *Psithyrus*-infested colonies, all of which possessed the old *Bremus* queen, none of the workers took to egg-laying.

On the first day (August 10) the *laboriosus* queen seized nearly every worker with which she came in contact and rolled the latter toward the ventral side of her abdomen, and made movements as if to sting her victim. This mauling, as a rule, lasted for only a few seconds, when the worker, which in every case was absolutely passive, was again released. In seizing the workers, both the mandibles and the first pair of legs were usually employed simultaneously, but on one occasion a worker was first lifted up by the pile of its thorax with the mandibles and then rolled below the body of the *Psithyrus*. None of the workers seemed to be any the worse for this mauling.¹

On the second day (August 11) the *Psithyrus* queen only occasionally seized a worker and treated it in the manner described. On the third day (August 12) this rough treatment of the *Bremus* workers became still less frequent, and thereafter the behavior of the *Psithyrus* queen and the *vagans* workers was quite peaceful.²

The attitude of the *Psithyrus* and the *Bremus* queen toward each other was somewhat different. From the very start the *Psithyrus* paid little or no attention to the latter, but during the first few days the *Bremus* queen avoided her rival whenever they met, and usually turned the tip of her abdomen toward the *Psithyrus*, as if to ward off an attack. However, these signs of hostility on the part of the *Bremus* queen gradually decreased and ceased completely after the fourth or fifth day, and thereafter both queens lived quite peacefully together.

To the *vagans* males, of which several were present when the *Psithyrus* first entered the nest, and to two young *vagans* queens which hatched on September 15, the *Psithyrus* paid no attention whatsoever, nor did any of these young queens and males exhibit the slightest sign of fear toward the *Psithyrus*.

¹ Sladen ('12, p. 253) who observed a *Ps. rupestris* queen, which he had placed in a *B. lapidarius* nest, treat the *lapidarius* workers in a manner similar to that described above, concluded that the workers were too small to get hurt, but, as will be seen later, this is not an adequate explanation.

² This agrees with similar observations by Smith ('55, p. 210) and Wheeler ('04, p. 353). According to the former, the *Psithyri* "live on the most friendly terms with the industrious part of the community," and the latter, in the case of ants, found that "the relations between the [*Formica*] *consocians* queen and the *incerta* workers were perfectly cordial."

As in the case of the *affinis-ashtoni* colony, the members of the *vagans-laboriosus* colony became more and more inactive as the weather grew colder. On September 12 the old *vagans* queen disappeared from the nest, and four days later the old *Psithyrus* vanished. The two had lived together for about five weeks.

From what has been said it is evident that *Ps. ashtoni* and *Ps. laboriosus* do not always, if ever, kill the host queen, and in this respect they behave like the two other American *Psithyri* whose hosts are known. One of these, *Ps. insularis*, was found breeding in a colony of *B. flavifrons* by Sladen ('15), and the other, *Ps. variabilis*, was found repeatedly in the nests of *B. pennsylvanicus* by Frison ('16). In the six infested nests reported by these two authors, each one contained the old *Bremus* queen, and this despite the fact that in both cases young *Psithyri* had emerged, or were about to emerge.

All of these observations on the habits of our American *Psithyri* agree with Hoffer's ('81, '88) account¹ and make Sladen's claim (that *Psithyrus rupestris* and *vestalis* always kill the host queen) extremely doubtful. Sladen ('12) based his conclusions on the fact that he never found a living *Bremus* queen in a *Psithyrus*-ridden nest.² Against this we have the positive evidence of Hoffer ('88, pp. 126, 148), who, as in the case of *Ps. campestris*, *quadricolor*, and *barbutellus*, also found the queens of *Ps. rupestris* and *vestalis* living in peace with the host queen, in one case after some of the offspring of the *Psithyrus* had emerged. Further inquiry into the queen-killing habit of *Ps. rupestris* and *vestalis* will undoubtedly show that Sladen ('99, '12, '15) based his conclusions on insufficient evidence.

This same criticism applies to another of Sladen's ('12) conclusions. He (p. 68) believes that *Psithyrus* queens do not kill

¹ Recent observations by Wheeler and Taylor ('21) indicate that *Vespa arctica* Rohwer, which has *Psithyrus*-like habits, being a social parasite on *Vespa diabolica* De Saussure, may also sometimes, if not always, live in peace with the host queen.

² Such negative evidence, as the work of Wheeler and Taylor ('21) indicates, is very unsatisfactory. Of nine *Vespa diabolica* nests taken by these two authors comparatively early in the season (before August 4), only one contained the old *diabolica* queen, and yet, with a single exception, these nests were not parasitized by *Vespa arctica*.

one another, because he never found a dead *Psithyrus* in a nest ruled by a *Psithyrus*. This certainly is not true of *Ps. laboriosus*. During June, July, and early August, *Ps. laboriosus* queens were very common in the vicinity of Boston, so that numerous experiments along this line could be carried out. The writer repeatedly caught *laboriosus* queens which were searching for *Bremus* nests and placed them in a small box containing comb filled with honey. Whenever two such queens were placed in this box, or in similar receptacles without comb, they immediately engaged in a violent battle which invariably resulted in the death of one of the combatants.

Psithyrus laboriosus queens also repeatedly appeared in several colonies of *Bremus fervidus* Fabricius and two of *Bremus bimaculatus* Cresson, one consisting of the old queen and about 25 workers, and the other of the old queen, several young queens, and about 50 workers. All of these colonies were kept on the third floor of one of the Bussey buildings. The *fervidus* colonies always expelled these intruders by a unique and very effective method, which will be described in another paper. The two *bimaculatus* colonies, on the other hand, never seriously objected to these intruders, and the latter sometimes stayed in their nests for several days. However, neither of the *bimaculatus* colonies produced any young *Psithyri*.

Psithyrus laboriosus queens which were searching for bumblebee nests were also frequently placed in these *bimaculatus* colonies. If a *laboriosus* queen was already present in the nest, and another one was introduced, the two *Psithyrus* queens usually clenched immediately, and within a minute or two, sometimes within a few seconds, one toppled over, mortally stung. In one or two cases the introduced *Psithyrus* queen tried to avoid a conflict by making a dash for the flight-hole as soon as she noticed the other *Psithyrus*. The two opponents, as a rule, seized each other by one of the legs and endeavored to sting one another. As soon as one had succeeded in penetrating the body of her adversary with her sting, she attempted to extricate herself from the embrace of her vanquished foe. During these encounters it sometimes happened that legs were torn off, or that the dead *Psithyrus* held firmly to one of the legs of the victor with her mandibles so that the latter had to be

released. Such a *Psithyrus* in turn was sometimes killed a few minutes later by a third *Psithyrus* which was placed in the nest.

The behavior of the *Psithyrus laboriosus* queens toward the *bimaculatus* workers differed essentially from that described for the *Ps. laboriosus* queen in the *vagans* colony. Every one of the 16 *laboriosus* queens used in these experiments completely ignored the *bimaculatus* queens and workers. Only once (shortly after she had been introduced into the nest) was one of these *laboriosus* queens observed raising one of her middle legs threateningly toward a *bimaculatus* worker, a form of intimidation which is quite frequent, even between members of the same *Bremus* colony.

Psithyrus laboriosus and *Psithyrus ashtoni* queens were also frequently placed in two strong colonies of *Bremus impatiens* Cresson, one having about 125 workers and the other more than 450. As soon as a *Psithyrus* queen was introduced into one of these nests, a great uproar arose in the colony. The workers rushed madly in every direction hunting for the source of the disturbance. The *Psithyrus* queen was seized almost immediately by numerous workers who tried to sting her, and was thus made absolutely helpless. A few bellicose workers, unable to get hold of the *Psithyrus*, seized some of the attached workers instead, and then attempted to sting toward the center of the struggling mass. During one of these experiments (August 15) such a fighting mass was lifted out of the nest box with a pair of forceps. When the workers finally released their hold, it was found that the mass had consisted of 17 workers and the *Psithyrus*. The latter and four of the workers were mortally stung. Although the *Psithyrus* made attempts at stinging during this struggle, one of the four workers was stung to death by one of its fellows at the periphery of the mass, and it is probable that the other three met death in the same manner. At the beginning of two of these experiments two workers, in their excitement, attacked each other (several inches from the *Psithyrus*) and one was stung to death. All of these experiments with the *B. impatiens* colonies always ended with the death of the *Psithyrus*.¹

¹ Frison ('21) reports that he found two *Ps. laboriosus* queens, one dead and one paralyzed, in the nests of *Bremus auricomus* Robertson and *B. pennsylvanicus*, and expresses the belief that both were stung to death by the

However, as will be seen from the following incident, a battle between a *Ps. laboriosus* queen and *B. impatiens* workers may have quite a different ending under somewhat different conditions. On July 24, 19 workers of colony No. 8 (*B. impatiens*), which had been transferred to one of the Bussey buildings on the preceding day, were caught at the old nest site and placed in a small glass jar. A few minutes later a *Ps. laboriosus* queen was discovered on some comb which had been left in the empty nest cavity of colony No. 9 (*B. fervidus*). Just to see what would happen, the *Psithyrus* was also placed in the jar. All of the inmates, including the *Psithyrus*, were ill at ease and tried to escape, but one or two of the *impatiens* workers nevertheless attacked the *Psithyrus* queen as soon as they came in contact with her. The latter now went on the warpath herself. She quickly seized one *impatiens* worker after another, whether attacked by them or not, rolled them below her abdomen and stung them to death. This done, she seemed to feel quite at home in the jar and began to lap up the honey which was oozing out from the bodies of her victims. From what has been said before, it is evident that this encounter would have ended quite differently if it had taken place in the nest of the *impatiens* workers. This, as well as some of his own observations (*e.g.*, '12, p. 277), disproves Sladen's ('12, p. 253) claim, already referred to, that the *B. lapidarius* workers, which were mauled by a *Ps. rupestris*, did not get hurt because they were too small.

During the summer of 1905 Wagner ('07, pp. 77, 78) discovered several nests of *Bremus muscorum* Linnæus at some distance above ground, and concluded that the nest-building instinct of this species, which normally builds on the ground, is in a process of transformation. The cause for this change he ascribes to natural selection brought about by the fact that the colonies of this species are destroyed, in large number, by various species of *Psithyrus*. It is improbable, however, that we are here dealing with a change in instinct. Hoffer ('88, p. 95) records that in the spring of 1886

Bremus queens, both of which he found uninjured. However, judging from the non-aggressive attitude of the queens, and the belligerent behavior of the workers of *Bremus impatiens*, the writer would suggest that the two *Psithyrus* queens were stung to death by the *Bremus* workers, which, according to Frison, were present in both nests.

three queens of *B. lapidarius*, which usually builds underground, started their nests in different parts of his house, and that a few weeks later numerous *Ps. rupestris* queens were hunting for these nests. These observations of Hoffer, and the fact that *Ps. laboriosus* queens repeatedly appeared in the writer's *Bremus* colonies kept in a third-story window (about 30 feet above ground), make it evident that *Psithyrus* queens are able to find bumble-bee nests, even if the latter are located at a considerable altitude. Natural selection in this direction is therefore of little benefit to a *Bremus* species as long as the members of the genus *Psithyrus* retain their acute sense of smell.

How exceedingly keen the olfactory sense of these social parasites actually is¹ can be inferred from the following observation: On July 3, an exceptionally pleasant day, colony No. 2 (*B. bimaculatus*) was dug up. The comb had hardly been exposed when a *Ps. laboriosus* queen swooped down upon it. She was captured and a half a minute later another *laboriosus* queen was buzzing about the comb. This one was also caught; but within another minute a third *laboriosus* queen alighted on the comb, and this despite the fact that not a single *Psithyrus* had been noticed in the vicinity previously.

This sudden appearance of the three *Psithyrus* queens also suggests an error in one of Sladen's ('12) experiments. As already stated, this author believes that the *Bremus* workers of a *Psithyrus*-ridden colony are constantly watching for an opportunity to kill the *Psithyrus*, even if the latter has been living with the colony for a considerable period. The observations on which Sladen ('12) chiefly based his conclusion were briefly as follows: On July 9, 1911, this author (cf. p. 251 ff.) dug up a nest of *B. lapidarius* containing 71 workers and a large amount of *Ps. rupestris* brood, but the *rupestris* queen was nowhere to be seen. Suspecting she had hidden herself in a side hole, he left a lump of cocoons in the nest cavity to attract her, and returning a quarter of an hour later actually found a *rupestris* queen on the comb, and concluded that he was dealing with the same *Psithyrus* queen which had been living in the nest. However, judging from Sladen's ('12, p. 253)

¹ Observations of Latter ('06) and the Raus ('18) indicate that this is also true of some solitary parasitic bees and wasps.

description of the hostile attitude of this *rupestris* queen toward the *lapidarius* workers, it seems probable that he was not dealing with the mother of the *Psithyrus* brood.

According to Hoffer ('81, '88), Friese ('88), and Sladen ('12), each European species of *Psithyrus* breeds only in the nests of certain *Bremus* species. Some—e.g., *Ps. rupestris* and *vestalis*—seem to be restricted to a single host, while others, like *Ps. campestris* and *barbutellus*, have two, or even three, hosts. Whether or not our American *Psithyri* have more than one host still remains to be decided. In determining this question we must understand clearly, however, what we mean by the term "host." While it is true that some of the European *Psithyri*—e.g., *Ps. rupestris*—breed only in the nests of a certain *Bremus* species, they may nevertheless be found lodging temporarily in the nests of other species. It will therefore be necessary, if we wish to avoid confusion, to restrict the term "host" to those *Bremus* species in whose nests a given species of *Psithyrus* is known to breed successfully. Using this definition of a *Psithyrus* host as a criterion, we thus far know of only one host for each of the four American species of *Psithyrus* whose hosts have been discovered. They are as follows:

TABLE I.

Psithyrus.	Host.
<i>Psithyrus ashtoni</i> Cresson.....	<i>Bremus affinis</i> Cresson
<i>Psithyrus insularis</i> Smith.....	<i>Bremus flavifrons</i> Cresson
<i>Psithyrus laboriosus</i> Fabricius.....	<i>Bremus vagans</i> Smith
<i>Psithyrus variabilis</i> Cresson.....	<i>Bremus pennsylvanicus</i> De Geer

But, as already pointed out by Sladen ('15), the geographical distribution of *Ps. insularis* and its host, *B. flavifrons*, are not identical, and we must therefore assume that *Ps. insularis* has more than one host, or that *B. flavifrons* also occurs in Saskatchewan, Manitoba, Ontario, Quebec, North Dakota, Minnesota, Wisconsin, Michigan, and New York. This second alternative is rather improbable.

Similar, though less extensive, discrepancies in the geographical distribution also exist in the cases of *Ps. ashtoni* and its host, *B. affinis*, and of *Ps. laboriosus* and its host, *B. vagans*. *Ps. ashtoni* either has more than one host, or *B. affinis* ought to be present on

Prince Edward Island, in New Brunswick, Nova Scotia, Quebec, Manitoba, and Saskatchewan. In this case it is difficult to make any prediction. *B. affinis* occurs in New England, Ontario, and Minnesota, and hence may yet be found in the adjoining eastern and central portions of Canada. This seems all the more probable when we consider that comparatively little collecting has been done in these parts of Canada, and that the number of *Bremus* species known from Illinois has been raised from 10 to 15 during the last few years by the intensive collecting of Frison ('19).

In the case of *Ps. laboriosus* and its host, *B. vagans*, we have to assume either that *Ps. laboriosus* has more than one host or that *B. vagans* is also present in South Carolina and Georgia and on Prince Edward Island. *B. vagans* occurs in Nova Scotia, North Carolina, and Tennessee, and it is therefore probable that it will be reported from the adjoining territories mentioned above.

In the case of *Ps. variabilis* and its host, *B. pennsylvanicus*, the geographical distribution of the former only covers a small portion of that of the latter, and it would therefore not be surprising if *Ps. variabilis* is taken in states from which it has not been reported. In fact, its known geographical distribution makes it almost certain that it occurs in Georgia, Indiana, and South Dakota.

There still remain several other interesting questions in regard to the members of the genus *Psithyrus*, such as origin, similarity in coloration with their hosts, and the frequency with which they breed in *Bremus* nests. The most extensive records which we have as regards the last of these three questions are those for one of the European species, *Ps. campestris*. Hoffer ('88, p. 132) records that he found more than 70 nests of *B. variabilis* and *B. agrorum* victimized by this species. Out of 48 nests of *B. variabilis*, 13 contained *Ps. campestris*, and during several summers in the early 80's about half of the nests of these two *Bremus* species harbored this parasite. In 1910 Frison ('16) opened seven surface nests of *B. pennsylvanicus*, four of which were infested by *Ps. variabilis*. Of the four *B. vagans* nests of which we have records (one each taken by Putnam, Beutenmueller, Franklin, and the writer), only one was later victimized by *Ps. laboriosus*, and of two *B. affinis* nests examined (one by Franklin and one by the writer), one was infested by *Ps. ashtoni*, while *Ps. insularis* was

found breeding in the only nest of *B. flavifrons* on record. These figures indicate that in some places, at least in certain years, about half of the colonies of those *Bremus* species which serve as hosts to certain species of *Psithyrus* are parasitized by the latter.

Some of the European *Psithyri*—e.g., *Ps. quadricolor* and *rupes-tris*—closely resemble their respective hosts in coloration, while others, like *Ps. campestris*, have no resemblance to their host whatsoever. In the case of the four American species of *Psithyrus* whose hosts are known we have a similar state of affairs. Between *Ps. laboriosus* and its host, *B. vagans*, there is considerable similarity, especially between *Psithyrus* male and host. On the other hand, there is little or no similarity between *Ps. ashtoni* and *insularis* and their respective hosts, *B. affinis* and *flavifrons*, and between *Ps. variabilis* and its host, *B. pennsylvanicus*, there is practically none.

Hoffer ('88, pp. 115, 116) states that those of the European *Psithyri* which are parasitic on *Bremus* species, which are equally large (queen against queen) or larger than they themselves, resemble their hosts more closely than those *Psithyrus* species which prey on smaller *Bremus* species. This correlation in color and size between parasite and host may be true of the European *Psithyri*, but it does not hold for our American species. According to Franklin ('12), the queens of *Ps. ashtoni* and *variabilis* are both considerably smaller than their hosts, *B. affinis* and *pennsylvanicus*, and still, in this case, there is little or no similarity in coloration between parasite and host. On the other hand, the *Ps. laboriosus* queen is somewhat larger than that of its host, *B. vagans*, and here, especially between *Psithyrus* male and host, we have a considerable degree of similarity.

We now come to the very interesting question as to the origin of the members of the genus *Psithyrus*. Müller ('71), Pérez ('83), Hoffer ('88), Sladen ('12), Lutz ('16), and Wheeler ('19), all of whom have paid more or less attention to this question, are agreed that the members of the genus *Psithyrus* are a degenerate offshoot from the genus *Bremus*.¹ One of these authors (Pérez, '83, pp.

¹ All observations on *Bremus*-*Psithyrus* colonies indicate that in no case is there a genetic relationship like that suggested by Patterson and Pack-Beresford ('03) for *Vespa austriaca* and *Vespa rufa*. According to this

207-215) believes that the representatives of the genus *Psithyrus*, because of their "perfect homogeneity," could not have come from several *Bremus* species, and, on the basis of structure, tries to show that they have all arisen from a single form which was closely related to *Bremus mastrucatus* Gerstæcker. He believes that in the course of time *Ps. barbutellus*, *campestris*, and *vestalis* became more differentiated from this original type than the other *Psithyrus* species. Hoffer ('88) and Sladen ('12), on the other hand, believe that there is no evidence for such an assumption, and the last-named author suggests that such resemblances as regards coat-color, etc., between several species of *Psithyrus* and their *Bremus* hosts are "clearly attributable to mimicry or exposure to the same conditions of life and not to ancestry." If we accept this explanation, it is difficult to account for those cases where there is not the slightest similarity between *Psithyrus* and host—e.g., *Ps. campestris* and *Bremus agrorum* Fabricius.

It is no doubt true, as Schmiedeknecht ('07) has pointed out, that in the case of the *Bremidæ* other criteria, such as length of head, are of greater taxonomic importance than coloration. That the latter is nevertheless of considerable value in determining relationship is indicated by the striking similarity between many of the species of the various English and American *Bremus* and *Psithyrus* groups, as they have been established by Franklin ('12) and Sladen ('12, p. 152), in the one case on the basis of structure, and in the other on the basis of habit (pollen-primers, pollen-storers, and carder-bees).

Using coloration as a basis, the various European and American *Psithyri* can be divided into three groups. The first of these, which may be called the *rupestris* group, is restricted to the Old World. The members of this group strikingly resemble a number of *Bremus* species, likewise restricted to the Old World, with one of which, *B. mastrucatus*, they are very similar in structure, as Pérez ('83) has shown. *Ps. rupestris*, the chief representative of this group, is parasitic on *B. lapidarius*, from which it is difficult to distinguish it.

theory, we should expect the parasitic Hymenoptera to be the ancestors of their hosts, a view which, as Saunders ('03) has pointed out, is difficult to harmonize with certain well-established facts.

Group two, which may be called the *laboriosus* group, and which comprises those *Psithyrus* species which Franklin ('12) has assembled under that name, is restricted to the New World. Here, again, we have a group whose members closely resemble a number of *Bremus* species, also restricted to the New World, one of which, *B. vagans*, serves as host to *Ps. laboriosus*, the chief representative of this group.

The third and largest group, which may be called the *vestalis* group, has representatives in both the Old and the New Worlds. To it belong such European species as *Ps. vestalis*, *distinctus*, and *quadricolor*, and the members of Franklin's ('12) *ashtoni* and *fernaldæ* groups in America. According to Pérez ('83) and Franklin ('12), many of the representatives of this group are also similar in structure. This group likewise closely resembles a number of *Bremus* species, which in this case are present in both the Old and the New World—e.g., *Bremus occidentalis* Greene in America and *B. latreillellus* and *jonellus* in Europe. The last-named species serves as host of *Ps. quadricolor*, a widely distributed European species belonging to this group.

The great difference in coloration (with a parallel difference in structure) between these three groups, the geographical distribution of those *Bremus* species which resemble them, and the fact that many *Psithyri* are parasitic on similarly colored *Bremus* species, all point to an independent origin of at least three *Psithyrus* groups.¹

Just how the parasitic habits of the representatives of the genus *Psithyrus* may have originated is suggested by certain observations of Sladen ('99, '12). According to this author, many of the later appearing queens of certain *Bremus* species do not take the trouble to start nests of their own, but enter nests already occupied by their own or other species. In the resulting conflict the foundress of the colony is sometimes killed, and her offspring then assists in rearing the brood of the intruder. He states that this occurs frequently between the queens of *Bremus lucorum* Linnæus and its larger variety, *B. terrestris*, the *lucorum* colony serving as a temporary host. From this temporary social parasitism, as he points

¹ A similar independent origin has been suggested by Wheeler ('10, p. 449) for certain ants which are temporary social parasites on other ants.

out, it is but a step to the permanent social parasitism of the members of the genus *Psithyrus*.²

This step in the probable evolution of the permanent social parasitism of *Psithyrus* is found among the ants. As Wheeler ('04, '10, '19) was the first one to point out, there is a large group of ants—e.g., *Formica consocians*—in which the queens are no longer able to found colonies of their own without becoming temporary social parasites on other ants, a form of parasitism which is intermediate between that of *Bremus terrestris* and *Psithyrus*.

SUMMARY AND CONCLUSIONS.

1. The American *Psithyri*, whose habits have been studied, rarely, if ever, kill the host queen.

2. A *Psithyrus laboriosus* queen which is searching for bumble-bee nests never tolerates another such *Ps. laboriosus* queen in the same *Bremus* nest.

3. During the first few days after a *Psithyrus laboriosus* queen has gained admittance to a nest of her host, *Bremus vagans*, the *laboriosus* queen intimidates the workers of the colony by rough treatment. After this period of "getting acquainted," the members of the *vagans-laboriosus* colony show no more hostility toward each other than the members of an uninfested *vagans* colony.

4. The *Psithyrus laboriosus* queen does not always, if ever, lay her eggs in a pollen mass in which *Bremus* eggs, or larvæ, are present, but, like the *Bremus* queen, constructs her own egg-cells and, like the latter, attaches them to one or more cocoons.

5. In *Psithyrus*-infested nests of *Bremus affinis* and *Bremus vagans* the destruction of the eggs, or young larvæ, of the host is probably caused by the *Psithyrus*, and not by her offspring.

6. It is not necessary for the *Psithyrus ashtoni* queen, and probably also not for other *Psithyrus* queens, to forage for her offspring in order that the latter may thrive.

7. The representatives of the genus *Psithyrus* have probably originated from several species of *Bremus* rather than from a single one.

8. Similarity in coloration between *Psithyrus* and *Bremus* spe-

² Wheeler ('10, p. 451) considers it probable that the permanently parasitic ants went through a similar evolution.

cies is probably due to genetic affinity, and not to "mimicry or exposure to the same conditions."

LITERATURE CITED.

Carpenter, G. H., and Pack-Beresford, D. R.

'03 The Relationship of *Vespa austriaca* to *Vespa rufa*. Ent. Month. Mag. (2), Vol. 14, pp. 230-242, 1 pl.

Franklin, H. J.

'12/13 The Bombidæ of the New World. Trans. Amer. Ent. Soc., Vol. 38, pp. 177-486, Vol. 39, pp. 73-200, 22 pls.

Friese, H.

'88 Die Schmarotzerbienen und ihre Wirte. Zool. Jahrb. Abt. Syst., Vol. 3, pp. 847-870.

Frison, T. H.

'16 Note on the Habits of *Psithyrus variabilis* Cress. Bull. Brookl. Ent. Soc., Vol. 11, pp. 46-47.

'19 Keys for the Separation of the Bremidæ, or Bumblebees of Illinois, and Other Notes. Trans. Ill. State Acad. Science, Vol. 12, pp. 157-166.

'21 *Psithyrus laboriosus* Fabr. in the Nests of Bumblebees (Hym.). Canad. Ent., Vol. 53, pp. 100-101.

Graenicher, S.

'05 Some Observations on the Life-History and Habits of Parasitic Bees. Bull. Wisc. Nat. Soc., Vol. 3, pp. 153-167, 1 pl.

Höppner, H.

'04 Zur Biologie der Rubus-Bewohner II. *Osmia parvula* Duf. et Perr., *Osmia leucomelana* K. und ihr Schmarotzer *Stelis ornatula* Nyl. Allgem. Zeitschr. Ent., Vol. 9, pp. 129-134, 2 figs.

Hoffer, E.

'81 Biologische Beobachtungen an Hummeln und Schmarotzerhummeln. Mitth. Naturw. Ver. Steiermark., Vol. 18, pp. 68-92.

'88 Die Schmarotzerhummeln Steiermarks, Lebensgeschichte und Beschreibung derselben. Mitth. Naturw. Ver. Steier., Vol. 25, pp. 82-159, 1 pl.

Illiger, K.

1806 Magazin für Insektenkunde. Vol. 5, pp. 1-370.

Kirby, W.

1802 Monographia Apum Angliæ. 2 vols. Ipswich.

Latter, O. H.

'06 How do Inquiline Bees Find the Nests of Their Hosts? Nature, London, Vol. 74, p. 200.

Lepeletier de St. Fargeau, A. L. M.

'32 Observations sur l'ouvrage intitulé: "Bombi Scandinaviæ Monographicè Tractati, etc., a Gustav. Dahlbom. Londini Gothorum, 1832"; auxquelles on a joint les caractères des genres *Bombus* et *Psithyrus*, et la description des espèces qui appartiennent au dernier. Ann. Soc. Ent. France, Vol. 1, pp. 366-382.

Lutz, F. E.

'16 The Geographic Distribution of Bombidæ (Hymenoptera) with Notes on Certain Species of Boreal America. Bull. Amer. Mus. Nat. Hist., Vol. 35, pp. 501-521.

Morice, F. D., and Durant, J. H.

- '14 The Authorship and First Publication of the "Jurinean Genera of Hymenoptera." Trans. Ent. Soc. London, pp. 339-437.

Müller, H.

- '71 Anwendung der Darwinistischen Lehre auf Bienen. Verh. Naturh. Ver. Preuss. Rheinl. u. Westphal., pp. 1-96, 2 pls.

Newman, E.

- '34 Attempted Division of British Insects into Natural Orders. Ent. Mag., Vol. 2, pp. 379-431.

Pérez, J.

- '83 Contribution à la Faune des Apiaries de France, 2^e partie. Act. Soc. Linn. Bordeaux, Vol. 37, pp. 205-378, 2 pls.

Putnam, F. W.

- '65 Notes on the Habits of Some Species of Humble Bees, and on the Leaf-cutting Bee. Proc. Essex Inst. Salem, Mass., Vol. 4, pp. 98-107.

Rau, Phil and Nellie.

- '18 Wasp Studies Afield. Princeton University Press.

Saunders, E.

- '03 On the Relationship of Aculeate Inquilines and their Hosts. Ent. Month. Mag. (2), Vol. 14, pp. 272-274.

Schmiedeknecht, O.

- '07 Die Hymenopteren Mitteleuropas. Gustav Fischer, Jenä.

Sladen, F. W. L.

- '99 Bombi in Captivity, and Habits of *Psithyrus*. Ent. Month. Mag., Vol. 35, pp. 230-234.
'12 The Humble-bee, Its Life-History and How to Domesticate it. Macmillan & Co., London.
'15 Inquiline Bumble-Bees in British Columbia. Canad. Ent., Vol. 47, p. 84.

Smith, F.

- '55 Catalogue of British Hymenoptera in the Collection of the British Museum. Part I, London.

Verhoeff, C.

- '92 Zur Kenntnis des biologischen Verhältnisses zwischen Wirt- und Parasiten-Bienenlarven. Zoöl. Anzeig., Vol. 15, pp. 41-43.

Wagner, W.

- '07 Psycho-biologische Untersuchungen an Hummeln mit Bezugnahme auf die Frage der Geselligkeit im Tierreiche. Zoologica, Vol. 19, pp. 1-239, 1 pl., 136 figs.

Wheeler, W. M.

- '04 A New Type of Social Parasitism among Ants. Bull. Amer. Mus. Nat. Hist., Vol. 20, pp. 347-375.
'10 Ants, their Structure, Development, and Behavior. Columbia University Press.
'19 The Parasitic Aculeata, a Study in Evolution. Proc. Amer. Philos. Soc., Vol. 58, pp. 1-41.

Wheeler, W. M., and Taylor, L. H.

- '21 *Vespa arctica* Rohwer, a Parasite of *Vespa diabolica* De Saussure. Psyche, Vol. 28, pp. 135-144, 3 figs.

